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When properly managed, the longleaf pine (LLP) savanna ecosystem is one of the most biologically diverse habitats in the world due to the high density of understory plant species. The ecosystem has played a vital role in building the economy and culture of the U.S. southeast over centuries, but anthropogenic influences (*e.g.* land conversion, logging, fire suppression, etc.) have decimated this ecosystem and the biodiversity it holds, making restoration a necessity. This study investigated the drivers of biodiversity in LLP-wiregrass (*Pinus palustris* Mill. – *Aristida stricta* Michx.) savannas at small ($1m^2$) and local ($25m^2$) spatial scales in order to provide crucial information and focus for restoration strategies, improving the management and health of LLP savanna. I collected species composition data along with various site and stand level characteristics at 15 study plots across North Carolina. Various regression analysis techniques were then used to identify potential drivers of biodiversity. This study found considerable variation in biodiversity and community composition across study plots, with small scale richness ranging from 2 to 11.8, and a regional richness of 143 species. Additionally, *A. stricta* was found to be a significant driver of biodiversity at both spatial scales, and a unimodal relationship between productivity and richness was found, which agrees with results found in other LLP-*A. stricta* savanna communities. The presence of this dominant grass species has a positive effect on biodiversity, but with increasing abundance, there is a decrease in every biodiversity metric, with the ideal relative cover of wiregrass being 16% for enhancing and maintaining biodiversity at small scales. If LLP savanna land

owners and managers can implement this ideal relative cover of wiregrass in their restoration strategies, the health and function can be restored to this ecosystem, as well as the biodiversity. Unfortunately, in today's society, restoring the economically important tree in the LLP ecosystem is often all that people focus on as it has direct monetary benefits. However, the understory provides numerous other provisioning services such as carbon sequestration and erosion and flood control, habitat for endangered species, and biodiversity itself. LLP savannas are so much more than the LLP tree that dominates the skyline, and understanding the drivers of the understory biodiversity will aid in the restoration of an essential component of this critically threatened ecosystem.

DRIVERS OF PLANT COMMUNITY BIODIVERSITY: UNDERSTORY DYNAMICS IN LONGLEAF PINE SAVANNAS OF NORTH CAROLINA

by

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CHAPTER I

INTRODUCTION

1.1 History and Ecology of the Longleaf Pine Ecosystem

Prior to European settlement of North America, the longleaf pine (LLP) savanna ecosystem covered an estimated 92 million acres in 9 coastal states across the southeast US (Frost 2006). This once dominant ecosystem is characterized by its open canopies and a continuous herbaceous understory predominantly comprised of graminoids (Harrington et al. 2013). This understory is immensely rich in grass and forb species making LLP savannas among the most biodiverse systems in the world (Brudvig et al. 2013). Additionally, LLP savannas are home to hundreds of endemic plant and animal species, some of which are federally listed as threatened or endangered (Walker, J. 1993). Areas with remarkably high richness are valued as biological conservation hotspots, especially if those areas are home to species that are threatened or endangered (Myers et al. 2000, Oswalt et al. 2012). As such, preserving the biodiversity and threatened species found in LLP savannas of the southeast US is of critical importance.

Broadly, the LLP savanna ecosystem is often described as an open, park-like system with the canopy consisting of a single widely spaced tree – the longleaf pine (*Pinus palustris*), for which the ecosystem gets its name. These LLP trees provide high quality timber and resin products, thrive in harsh areas, resist insects, and are fire-tolerant

(Johnson and Gjerstad 2006). While the canopy is low in diversity, the understory is immensely rich. Due to geographical and environmental variation across the LLP range, the composition of vegetation changes, as does the diversity of the understory. There are many ecological classifications of LLP vegetation across the 9 coastal states in the southeast, and each community type is associated with different levels of biodiversity (Peet 2006). Plant species richness is typically highest in mesic LLP savannas and seepage wetlands near the coast line, as opposed to more xeric, upland sites. Previous research has found at a $1m^2$ spatial scale, an average of 22.4 species in LLP savannas of North Carolina and only an average of 3.2 species in xeric uplands of North Carolina. This large difference in species richness across community types is also seen at other spatial scales. At smaller spatial scales of $0.01m^2$, xeric uplands and savannas of NC contain an average richness of 0.5 and 4.4 plant species, respectively, and at larger spatial scales of $1000m^2$, xeric uplands and savannas of NC contain an average richness of 22.5 and 94.4 plant species, respectively (Peet 2006).

Across the LLP ecosystem range, grasses dominate the understory, and as this is a fire-dependent system, bunchgrass species are essential to the even spread of fire across the surface of the understory, and therefore, essential to the maintenance of biodiversity. The dominant bunchgrass species varies across the LLP ecosystem range, with *Aristida stricta* (Carolina Wiregrass) dominating from Virginia to northern South Carolina, *Aristida beyrichiana* (Southern Wiregrass) dominating from southern South Carolina to Northern Florida, and various *Andropogon* (Bluestem) species dominating the western range of LLP (Peet 2006). Bunchgrass species, such as *A. stricta* (wiregrass), are not

dominant in the competitive sense, but dominant in terms of abundance in the understory (Roth et al. 2008, Myers and Harms 2009). In LLP-wiregrass savannas, wiregrass is sometimes thought of as a keystone species because of its essential role in structuring the understory through its effect on fire behavior. However, the relatively high abundance of wiregrass in LLP understories indicates that this bunchgrass is not a keystone species, rather an autogenic ecosystem engineer (Jones et al. 1994). Therefore, maintaining a sufficient foliar cover of wiregrass in the understory to promote fire is critical to maintaining biodiversity and the health and function of the LLP ecosystem.

Both the LLP tree and the understory are fire-adapted. In fact, prescribed fire is a critical component to LLP savanna health, and often fire return intervals (defined as: how often fire moves across the landscape), are managed to be quite short (every 2-3 years). Previous research demonstrates that fire regimes with intermediate levels of disturbance are optimal for the maintenance of LLP understory communities as dead tissues and debris are burned away and new plants are able to grow with increased resources (Brockway et al. 2006). This creates a positive feedback loop with understory grasses, paired with fallen pine needles, facilitating the ignition and spread of future fires (Brockway et al. 2005). Additionally, the fire limits woody shrubs and hardwood trees (Landers 1991), ensuring the open, park-like stand structure which enhances biodiversity of the understory.

Unfortunately, much of the biodiversity has been lost as currently, less than 3% of natural stands in the historic range of the LLP ecosystem remain (Figure 1; Oswalt et al. 2012). This extensive loss makes LLP savannas one of the most endangered ecosystems in the U.S. (Noss et al. 1995). The once thriving, diverse LLP communities were replaced with monotypic plantations, agricultural fields, human infrastructure, or were fire suppressed yielding entirely different plant communities (Frost 2006).

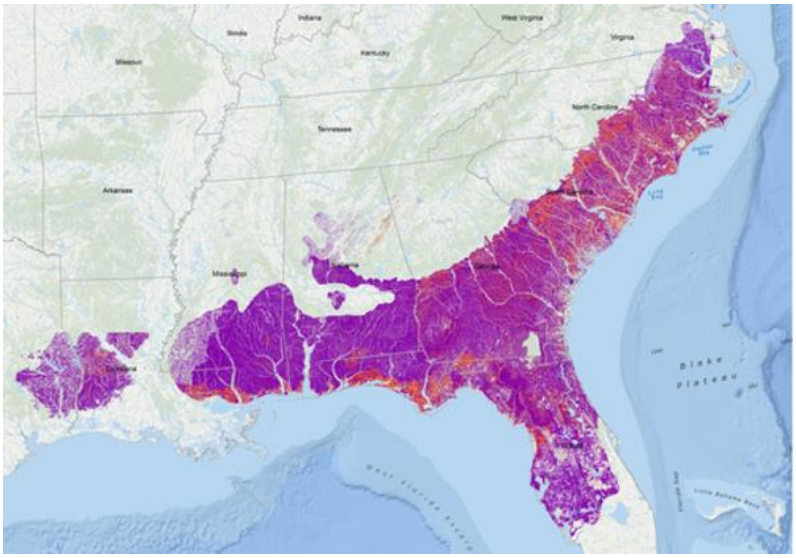


Figure 1. The Historic Range (purple) of the LLP Ecosystem in the Southeastern US, Which Covered ~92 Million Acres. Today, That Range Has Been Reduced to Less Than 3% of the Original Cover (red). Map Modified From (Cerame et al. 2014). Original Data from NatureServe and LandScope America.

The extensive loss of the ecosystem has been attributed to multiple anthropogenic causes (Outcalt et al. 1999, Van Lear et al. 2005, Frost 2006). For example, agriculture has always been an important part of the Southeast's economy (Frost, 2006), with many LLP lands converted for that purpose. Over time some of those agricultural lands were abandoned because the soil was either too wet or too dry for agriculture, leaving legacies

that persisted for years, with altered biodiversity, the absence of important species, and the presence of invasive species (Flinn and Vellend 2005, Walker and Silletti 2006, Brudvig et al. 2013a).

Simultaneous to agricultural expansion, the demand for timber and naval stores (tar, pitch, and rosin used to maintain wooden ships of that time) exploded, and the naval stores industry thrived in much of the southeast. Naval stores predominantly came from the LLP tree (Frost 2006). This industry particularly thrived in North Carolina, which quickly became known as the "Tar Heel State", a moniker still used and widely recognized today (Outland III 2004).

As the exploitation of LLP trees continued through the 19th century, it became apparent that most cutover and abandoned lands were not successfully regenerating LLP. Eventually pulp mills and the exploitation of smaller, faster-growing pine tree species became popular, and by the 1990s, the area occupied by LLP savanna was only 5% of the original extent (Oswalt et al. 2012). For there, fire suppression in the early twentieth century reduced the remaining LLP savannas even further. Fire suppression allowed secondary species the chance to grow in many LLP savanna stands across the range, creating mixed hardwood forests (Outland III 2004) with a dense over-growth of woody species. These woody species outcompeted the original ground cover, and diversity plummeted (Frost 2006). In fact, fire suppression and the growth of woody species changed the system so much that the LLP savanna was often eliminated and replaced with a hardwood forest.

However, in recent years, there has been a push to restore LLP communities. Restoration of LLP is a collaborative, cross-disciplinary, effort from state and federal agencies, private industry, universities/research agencies, private landowners, and non-governmental organizations. The main goal of many of these efforts is to reestablish LLP as a significant component of the Southern landscape, but other goals include the introduction of prescribed fire, reestablishment of groundcover species, reintroduction of native animal communities, boosting local economies, and regaining the lost biodiversity. To encourage LLP restoration, the Departments of Agriculture, Defense, and Interior signed a memorandum in 2010 that promoted the range-wide establishment of an additional 5 million acres of LLP by 2025 (Oswalt et al. 2012). Successful restoration of the diverse LLP savanna understory necessitates scientific investigation into the ecological drivers of understory plant dynamics in these communities. Knowing what maintains and enhances wiregrass and all other components of biodiversity will allow restoration practitioners to target specific ecological drivers and processes for restoration.

1.2 Research Goal and Rationale

Here, the primary goal was to ***understand the ecological drivers of biodiversity and plant community dynamics in LLP understories*** with the aim of providing critical data to empower and inform the restoration of this iconic ecosystem. Specifically, this thesis focused on the LLP savannas that span North Carolina (NC). In the literature, the vast majority of research regarding the understory of LLP savannas occurs in states with a larger component of LLP, such as Georgia or Florida. Further, the research that has occurred in NC has been either on Fort Bragg Military Reservation or in Green Swamp

Preserve, almost exclusively. Therefore, this study was conducted on NC LLP sites other than the ones listed above.

LLP savanna is simultaneously one of the most diverse and one of the most threatened ecosystems in the US, and it is a system which provided the Southeast with great services. It is often said that the LLP tree is the tree that built the South, it gave North Carolinians their nickname, “the tar heels”, and it even begins the state toast “here’s to the land of the longleaf pines…”. While being instrumental in the building of the South, sadly, many modern-day North Carolinians do not even know what LLP savanna is, assuming the hardwood forests of today are the natural state. Luckily, substantial effort is being made to restore this iconic ecosystem to the land it once covered. Significant knowledge on the drivers of the LLP tree itself has been obtained through years of research for the logging industry. However, the substantial biodiversity and numerous ecosystem services supplied by LLP savannas are due to the understory. Research on the drivers of understory dynamics severely lags behind the research on the dominant tree. This thesis aims to help close this knowledge gap. Once the factors driving the understory dynamics are understood, LLP savanna can be managed more effectively and restored more efficiently, with their former diversity and function regained. The primary goal was addressed through two major objectives.

1.3 Objective 1

The first objective of this thesis was to **describe the biodiversity and community dynamics seen in the herbaceous understory layer across LLP savannas in NC at small, local, and regional spatial scales**. Specifically, multiple aspects of biodiversity were explored, including richness, evenness, and diversity. In addition, other components of the understory system were explored, such as aboveground net primary productivity (ANPP) and dominance, including the abundance of wiregrass (*A. stricta*) which is necessary for optimal burning of the understory. Biodiversity is often described in the literature using only one metric, species richness (Beckage and Stout 2000, Brudvig and Damschen 2011, Costanza et al. 2011). However, this metric alone is an inadequate descriptor as biodiversity is multifaceted. Restoring the understory of LLP savannas is about more than obtaining a number of species. We must aim to restore understory dynamics as a whole, targeting dominant species and ecosystem processes, in addition to richness.

Productivity (ANPP) is the rate at which energy is stored as biomass, and it is an important ecosystem process that has received much attention, and that varies across different ecosystems. The literature suggests a strong relationship between productivity and biodiversity, and therefore in the diverse LLP savanna ecosystem, that relationship and the variation in productivity must be explored. Previous research on the diversity of the understory in the LLP ecosystem has focused on smaller spatial scales ($1m^2$) as well as larger scales of $100m^2$ and $1000m^2$ (Brudvig and Damschen 2011, Brudvig et al. 2013b). Dell et al. (2019) found that community diversity was maximized at small spatial

scales and suggests that vegetation sampling should be done at $1m^2$ as this scale captures the most diversity. Here I focused on small spatial scales ($1m^2$) in order to capture the most diversity, as well as local spatial scales ($25m^2$), as studies at this scale are lacking, and likely to be extremely informative to private land restoration practitioners which may be working on local scales.

1.4 Objective 2

The second objective of this thesis is to **explore the drivers of biodiversity and community dynamics across LLP savannas in NC at small and local spatial scales**. The strength to which environmental factors influence biodiversity and community dynamics in LLP savanna understories of NC at small and local spatial scales lacks deep understanding and will be of great value as restoration of this system is a high management priority (Oswalt et al. 2012). This objective has several key parts.

First, I will identify factors associated with the variability in biodiversity, productivity, and wiregrass cover seen across the landscape at multiple spatial scales. There are many abiotic factors that influence plant community dynamics, including light and nutrient availability, precipitation, fire, temperature, elevation, etc. (Peet, 2006). These factors are known to limit plant species presence and growth (Chapin et al. 1987), and are therefore explored as potential drivers of understory dynamics in the LLP savannas of NC. LLP savannas in NC occur on a variety of sites ranging from mesic to xeric, with wide variation in soil type and texture, and nutrient availability. The variability yields differing plant communities across the landscapes of NC (Peet 2006).

Second, I will investigate the relationship between productivity and biodiversity. The relationship between aboveground net primary productivity (ANPP) and plant species richness has been investigated in many ecosystems and at different spatial scales. The directionality of the relationship varies and has been described as positive, negative, unimodal, and having no relationship (Rosenzweig 1995, Waide et al. 1999, Gough et al. 2000, Chalcraft et al. 2009). In the LLP savanna ecosystem, researchers have found a positive relationship in communities where the dominant grass species is *A. beyrichiana* (Kirkman et al. 2001) and a unimodal relationship in communities where the dominant grass is *A. stricta* (Walker and Peet 1984). In this study, I explored the relationship between productivity and biodiversity, specifically richness, at two different spatial scales. As this study was conducted in LLP-*A. stricta* communities, we expected to see the same unimodal relationship as seen in the study by Walker and Peet (1984).

Lastly, I will explore the drivers of the dominant species, *A. stricta* (wiregrass), as well as the influence it has on understory dynamics. In these LLP-wiregrass savannas, system function is maintained by the wiregrass in the understory. The flammable, resinous LLP needles shed from trees, and the long, thin leaves of this bunchgrass species provide the fuel for frequent, low-intensity fires that move rapidly across the surface of the landscape (Outcalt et al. 1999). Therefore, because of its role in biodiversity-ANPP relationships and its ecological importance for proper functioning of the LLP savanna system, the niche of this dominant grass species in NC LLP savannas will be described.

CHAPTER II

METHODS

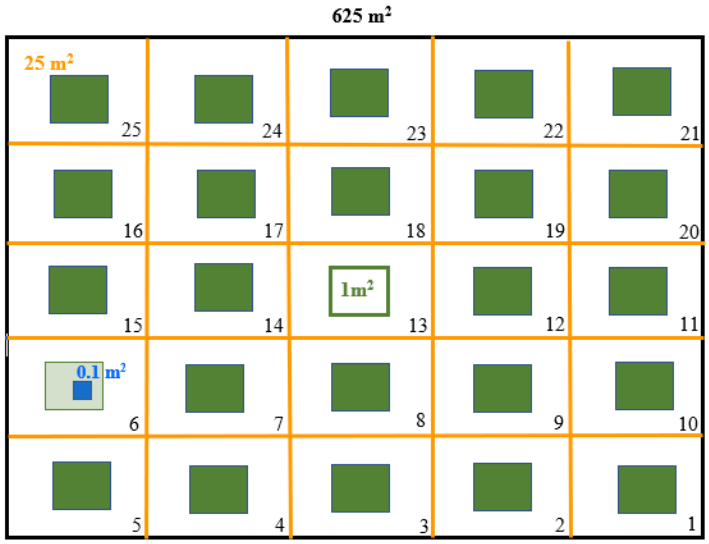
2.1 Study Area

This study was conducted in North Carolina on 15 sites spanning from the Sandhills, eastward to the Outer Coastal Plain (Figure 2). Ten sites were located in the Sandhills region on the Sandhill Game Lands, Weymouth Woods-Sandhills Nature Preserve, Calloway Forest Preserve, and Carvers Creek State Park. Two sites were located in the Inner Coastal Plain at Bladen Lakes State Forest, and three sites were located in the Outer Coastal Plain at Croatan National Forest. These three ecoregions vary in growing season (April-October) temperature and precipitation amounts (Table A1), as well as elevation, taxonomic soil type and community classification (Table A2), creating gradients of abiotic and biotic drivers across my 15 plots.

Figure 2. The Location of the 15 Study Plots Within the Sandhills (red), Inner Coastal Plain (blue) and Outer Coastal Plain (purple) in North Carolina.

2.2 Experimental Design

A single plot (625m^2) was established at each of the 15 sites in LLP-dominated stands (Figure 3). Plots were established at relatively level locations and at least 15m from any road ways or foot paths to avoid edge effects. Within each 625m^2 plot, 25 subplots (each 25m^2) were arranged in a grid.



BLACK: Plot (25 X 25 m) = 625m^2
ORANGE: Subplot (5 X 5 m) = 25m^2
GREEN: Quadrat for species identification (1 X 1 m) = 1m^2
BLUE: ANPP clippings (0.5 X 0.2 m) = 0.1m^2

Figure 3. Experimental Design of All Study Plots (n=15). Within Each 625m^2 Study Plot (black), 25 Subplots (each 25m^2, orange) Were Arranged in a Grid. Within Each Subplot, There Was a 1m^2 Quadrat (green) in Which I Recorded Species Composition, and Within Each Quadrat, There Was a Nested 0.1m^2 Quadrat (blue) Used for Destructive Sampling of ANPP.

2.3 Vegetation Surveys

Inside each subplot (n=25), a 1m^2 species composition quadrat (Figure 3) was established and permanently marked with flags. Quadrats were placed in the center of subplots and in the rare case that a large canopy tree fell within normal quadrat

placement, quadrats were shifted slightly off-center to exclude the tree base. In each quadrat, all plants were identified to species, and percent cover was estimated in both the early and late growing season. The maximum cover obtained from the two time points for each species was used in all analyses.

Additionally, in each 5x5m subplot, tree and shrub species of the over- and mid-story were documented via several measurements since their presence and associated canopy cover are known to influence species richness and understory community composition (Baldwin et al. 1996, Harrington 2006). First, LLP trees with a diameter at breast height (DBH) greater than 10cm were recorded as alive or dead, as well as their DBH. Second, if LLP trees were shorter than 1.37m and/or had a DBH less than 10cm, presence was recorded. Third, shrub species were recorded in each subplot as well as the number of stems coming out of the ground in order to accurately describe mid-story cover; only recording occurrence of shrubs would not account for the varying cover of each, which is critical to understanding their influence on the understory.

2.4 Vegetation Clipping for ANPP

Late in the growing season, ANPP was estimated by clipping all aboveground herbaceous biomass in one $0.1m^2$ quadrat nested within each $1m^2$ quadrat (n=25). All plants within the nested quadrat were clipped at ground level with scissors and sorted by growth form and live versus dead tissue (grass, woody, forb, past year's dead, and LLP needle litter). ANPP clippings were put into paper bags and transported back to the UNCG lab where they remained in a forced air oven at 60°C for a minimum of 48 hours until dry weights were measured and recorded.

2.5 Abiotic Measurements and Soil Nutrient Testing

Abiotic variables were measured to account for the influence of environmental conditions on understory plant communities. Photosynthetically active radiation (PAR) was measured with a ceptometer in each subplot by taking the average of 3 light readings at standing level to see how much light reaches the understory, and the average of 3 corresponding readings under the grass and forb canopy to see how much light reaches the ground. Before taking readings, the ceptometer was calibrated, and open-sky readings were obtained as a reference light condition for each plot.

Due to the strong influence of soil nutrients on community composition and species abundance, soil samples were taken in each subplot to help account for variations in composition across the plant communities of each plot. Soil samples were collected from multiple locations within each subplot using a soil core sampler to a depth of 10cm (Baldwin et al. 1996). Soil samples were brought back to the lab and put into a forced air oven at 35°C until ready for chemical analysis. Samples were taken to the North Carolina Department of Agriculture & Consumer Services Agronomic Services Division in Raleigh, North Carolina and tested for pH, phosphorous, potassium, calcium, magnesium, sodium, manganese, copper and zinc. The analysis of nitrogen was not included in this free service and therefore soil nitrogen levels were unfortunately not addressed in this study.

Several variables were measured at the plot level. Elevation of each plot above sea level was recorded using USGS TNM elevation data. Additionally, we collected burn data from site managers, specifically the number of years since the last burn, as fire has a

vital part in the restoration of LLP across its entire range. To account for natural variation in vegetation across landscapes, each plot was grouped by region of North Carolina (Sandhills, Inner Coastal Plain, or Outer Coastal Plain) and then climate data per region was extracted from US Climate Data (https://www.usclimatedata.com). I focused on weather data from the growing season (April-October) of each region. This included total growing season precipitation (mm) and average high and low temperatures (°C) during the growing season.

2.6 Statistical Analyses for Objective 1

Diversity was measured and compared within and across plots by calculating species richness and evenness. Evar, a metric that is independent of species richness, was used as the measure of evenness at every subplot, Simpson's dominance index (inverse of Simpson's diversity) was used to measure diversity at every subplot, and Berger-Parker dominance index were used to assess dominance at every subplot. To calculate these biodiversity metrics at a larger spatial scale (*i.e.* at the plot level), two approaches were taken. The first approach was to average biodiversity metrics across subplots to represent the mean values of a given plot at a $1m^2$ scale. The second approach was to sum the species composition data across subplots yielding a single $25m^2$ plot, and then to calculate total biodiversity metrics for each plot. By calculating total biodiversity metrics of a plot, we were able to capture the biodiversity of the understory at the local spatial scale in its entirety, instead of only averaging our small scale ($1m^2$) species composition data up to the local scale. Aboveground net primary productivity (ANPP) in each subplot was calculated by summing the weights of biomass in the functional groups graminoid,

forb, and woody. This subplot estimate was then totaled for each study plot to get a value of total ANPP per plot. Additionally, mean ANPP for the 15 study plots was calculated by averaging the total biomass of all subplots within a plot. The coefficient of variation (CV) was calculated for ANPP, relative wiregrass cover, and richness in each plot, to describe the variability within each study plot. Calculating the CV of these variables provides information on their heterogeneity within and across my study plots.

Multiple exploratory analyses and data visualizations were used to address objective 1. First, a Bray-Curtis dissimilarity matrix was created comparing all subplots (n=373) to each other and nonmetric multidimensional scaling (NMDS) was used to visualize the variation within and across LLP understory communities that were studied. Subplots were then averaged, and the centroid of each plot (n=15) was depicted using NMDS. For the NMDS showing plot centroids, error bars summarize all the replications within each plot (n=25). NMDS was used because it is a useful tool in combining information from multiple dimensions into just a few, so that they can be more easily visualized. Permutational multivariate analysis of variance (PERMANOVA) was used on the study plots (n=15) to test the hypothesis that the centroids and dispersion of the groups are not equivalent between plots. The distances between replicates (*i.e.*, subplots) and the centroid (dissimilarity within plots) and the distances between centroids (dissimilarity among plots) were then calculated. A pairwise SIMPER analysis was then used to identify the plant species in the understory that contribute most to the differences between all study plots.

It has been suggested that species richness and evenness alone are inadequate metrics to describe communities, but in conjunction with Rank Abundance Curves (RACs), community composition and structure can be clearly described (Avolio 2015). RACs were constructed to visualize different aspects of community change (richness, evenness/dominance, and species rank differences) and were compared across all study plots utilizing CoDyn 2.0 (Avolio et al. in prep). Comparing metrics of biodiversity and visualizing these metrics through RACs helped to describe how diversity and composition vary across these communities.

2.7 Statistical Analyses for Objective 2

To explore how abiotic and management variables collected control different aspects of the understory dynamics, linear and multiple linear regressions were used. We focused on a small subset of the potential predictor variables that were collected, as many of them covaried. Light availability at standing level and light availability at ground level were highly correlated ($r = 0.816$) as were growing season average high temperatures and elevation with growing season precipitation ($r = 1.0$ and $r = -0.837$, respectively). Therefore, the variables omitted from analyses were light availability at standing level, average high temperatures in the growing season and elevation. Light availability at the ground level was kept in analyses because it tells us how much light reaches the small forb species in the understory, where the majority of the diversity occurs, and growing season precipitation was kept because it directly affects plant growth and viability.

Before running linear regression analyses with soil nutrient data, the soil characteristics (pH, phosphorus, potassium, magnesium, calcium, manganese, zinc,

copper, sulfur, & sodium) of each subplot were combined into principal components using principal component analysis (PCA; Figure 4).

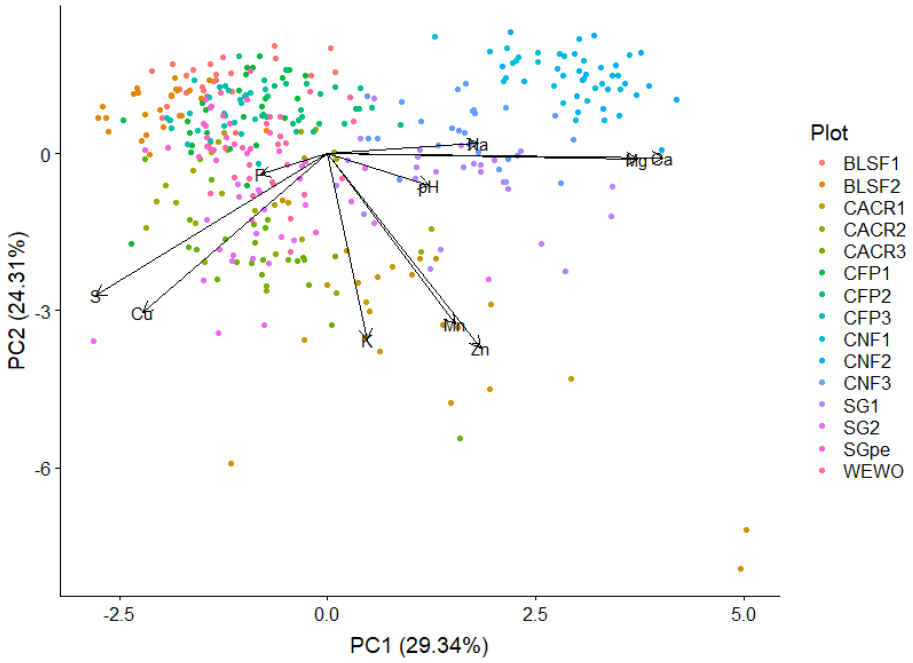


Figure 4. Principal Components Analysis (PCA) Plot of Nutrient Data at a Small Scale ($1m^2$).

Then, PCA axis 1 (PC1) which accounted for 29.3% of the cumulative variance among the data, was used in the regression analyses. The final set of predictor variables used in analyses were growing season precipitation, principal component 1 (PC1) for soil nutrients, light availability at ground level, litter cover (pine needle weights), aboveground net primary productivity, number of LLP trees, relative wiregrass cover, number of shrub/scrub-oak stems, and the time (years) since the plot was last burned.

Bivariate linear regressions of each predictor variable were performed on the different biodiversity metrics (richness, the inverse of Simpson's diversity, evar, and

Berger-Parker dominance), as well as on relative wiregrass cover and ANPP at the subplot level. Relative wiregrass cover and ANPP were included as response variables because we suspect they are drivers of biodiversity in LLP-wiregrass savanna understory communities, and therefore, addressing the influence of our predictor variables on these metrics tells us what drives them and in turn, what is driving biodiversity. Following bivariate analyses, a multiple regression model of all predictor variables on relative wiregrass cover was constructed in order to determine the drivers of wiregrass cover in the understory and to describe the ecological niche of wiregrass. Then, to test for the inherent correlation of the response variables between plots, the study plot was included as a random effect in linear mixed effect modeling. Then, I performed polynomial multiple regression of ANPP and relative wiregrass cover, separately, on richness at the small, subplot scale. To examine relationships at the plot level, bivariate linear regressions of predictor variables on mean and total biodiversity metrics were used. At the plot level only, I also calculated the coefficient of variation for ANPP, wiregrass cover, and richness, and these CVs were then used in regression analyses to see which, if any of our explanatory variables, is driving variability across these understory communities.

CHAPTER III

RESULTS AND DISCUSSION

3.1 Objective 1

Overall, I found large variability in plant community characteristics and function across the 15 sites. The relative cover of the dominant grass species, *A. stricta*, varied greatly within and across plots (Figure 5a and c, respectively), ranging from 0% to 100% relative cover at both the subplot and plot level, with most subplots having ~30% relative cover (Figure 5a). Richness was also variable, with subplots containing 5 different plant species being the most abundant (Figure 5b), and plots containing 25 species in total being the most abundant (Figure 5d). Additionally, the total plant species richness found at a regional scale (across all 15 study plots) was 143.

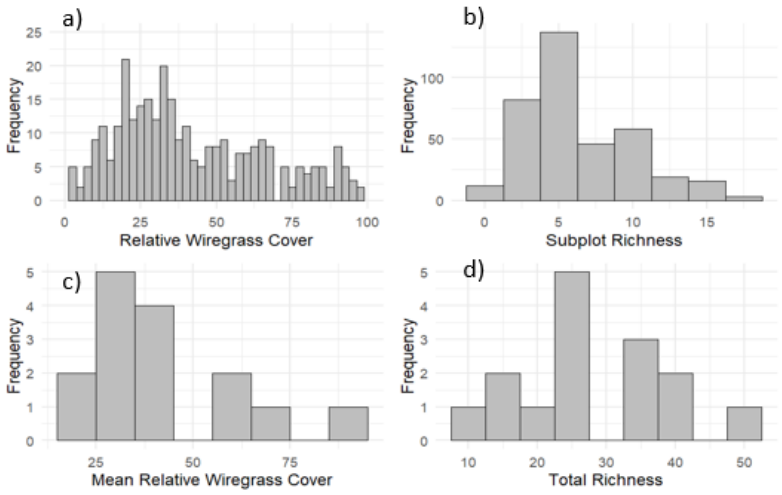


Figure 5. Variability of Relative Wiregrass Cover and Species Richness at Small Scales ($1m^2$; a and b respectively) and at Local Scales ($25m^2$; c and d respectively).

When taking into account both species identity and abundances of the whole community in multivariate space, there is also a substantial variation in the understory communities within (Figure 6a) and across (Figure 6b) all of my study plots. Subplots within a given plot seemed to vary more along the NMDS1 axis than the NMDS2 axis (Figure 6b error bars) potentially suggesting that different plant species play a role in within site variability compared to across site variability. Interestingly, plots in the Sandhills tended to fall out positively on axis 1 whereas plots in both the Inner and Outer Coastal Plain tended to fall out more negatively along axis 1. The average distance to the median varied across study plots, regardless of the ecological region in which they were located (Table 1). PERMANOVA analyses confirmed that indeed, among plots, centroids were significantly different ($F=17.32$, $p=0.001$), and that within plots (subplots), the dispersion around centroids was also significantly different ($F=15.34$, $p<0.001$; Figure 7).

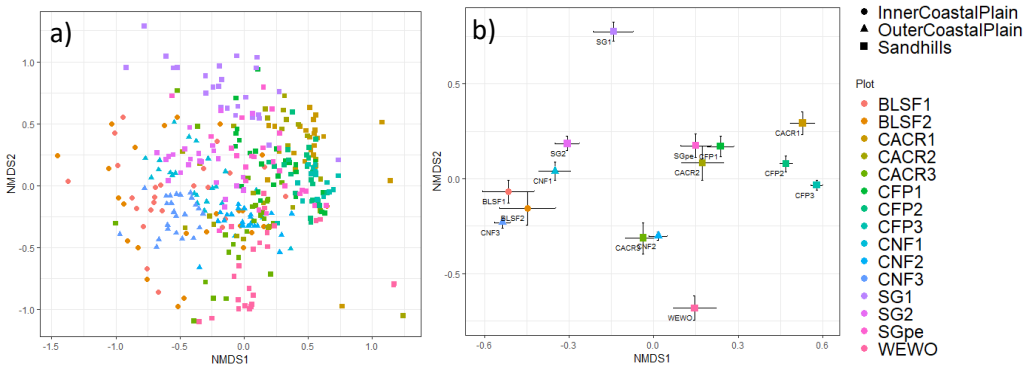


Figure 6. NMDS Showing a) All Study Plots (n=373) and b) Averaged Subplot Scores Per Plot (n=15). Shapes Represent Geographic Region and Colors Represent Each of the 15 Plots. Stress = 0.25.

Table 1. Beta Diversity Described by the Average Distance to the Median of All Study Plots.

Plot Code	Average Distance to Median
SG1	0.4999
SG2	0.3713
SGpe	0.3737
WEWO	0.4972
CFP1	0.3169
CFP2	0.2435
CFP3	0.2421
CACR1	0.3938
CACR2	0.4624
CACR3	0.4539
BLSF1	0.4786
BLSF2	0.4801
CNF1	0.3116
CNF2	0.3345
CNF3	0.3569

Similarity percentage (SIMPER) analysis highlighted the cumulative differences between plots and the specific species causing the variation between them. The species that occurred the most with the highest cumulative contribution to plot differences was *Robinia nana*, a low-growing deciduous shrub, typical of the Sandhills, with an average contribution to plot differences of 72%. The next most common species with high cumulative contributions were *Andropogon virginicus* (72.4%), a common bunchgrass, and *Pteridium aquilinum* (72.2%), a fern found in xeric sites. These three species showed large variation across plots, with some plots having high abundance and even being typified by the presence of these species, while in other plots, these species were completely lacking.

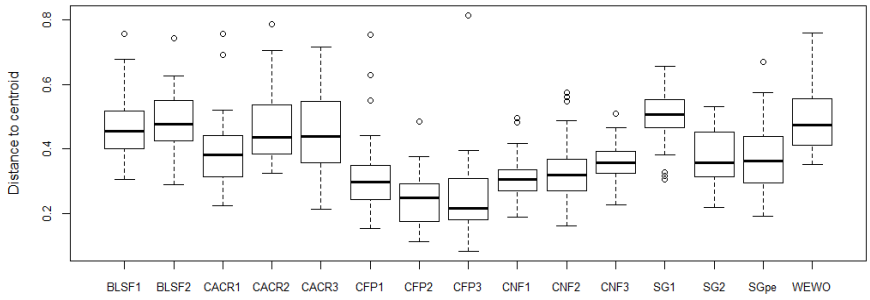


Figure 7. Dispersion of Subplots Within Study Plots. Plots That Have the Highest Average Distance to Centroid Are the Plots Where the Subplots Are Most Variable in Species Identity and Abundances. Boxplot Whiskers, or the Extremes of the Dotted Lines, Represent the Range in Distance for Each Plot.

The rank abundance curves (RACs) show variation in richness, evenness, and dominance between plots, with *A. stricta* having the greatest abundance in 9 of the 15 study plots (Figure 8). Many plots were composed of a high number of forbs (shown in pink) and graminoid species (shown in green). These curves also indicate that plot richness is not correlated with the level of dominance in a plot. For instance, plot CNF2 is greatly dominated by *A. stricta*, but the length of its RAC is shorter than many of the others, meaning that there were less species present. Conversely, CNF1 also has dominance by *A. stricta*, but the length of its RAC is longer than many others, meaning that there were more species present.

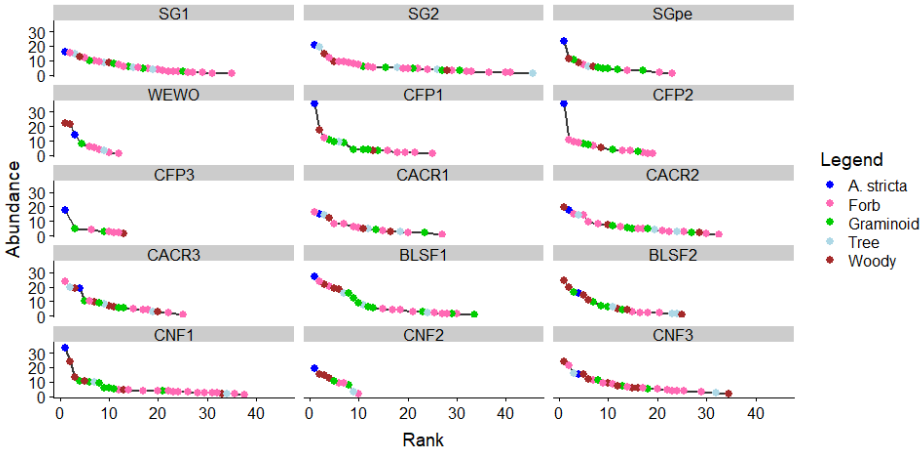


Figure 8. Rank Abundance Curves (RACs) for the 15 Study Plots from the Western Most Plot to the Eastern Most Plot.

The calculation of biodiversity metrics also showed the variability across and within my study plots (Table 2). There was considerable variation across subplots ($1m^2$), as well as across the 15 study plots ($25m^2$), with subplot richness ranging from 1 to 17 species, mean richness ranging from 2 to 11.8, and mean diversity ranging from 1.37 to 6.46 per m^2 (Table 2). Totaled biodiversity metrics, summarized in Table 3, show that the plot with the highest mean richness (plot code SG2 from the Sandhills) is also the plot with the greatest total richness (S=49). There were significant differences between each ecological region in both richness ($F = 26.07$, $p < 0.001$; Figure 9) and diversity ($F = 31.17$, $p < 0.001$). While these differences could be due to numerous regional differences, a likely culprit is the difference in growing season precipitation.

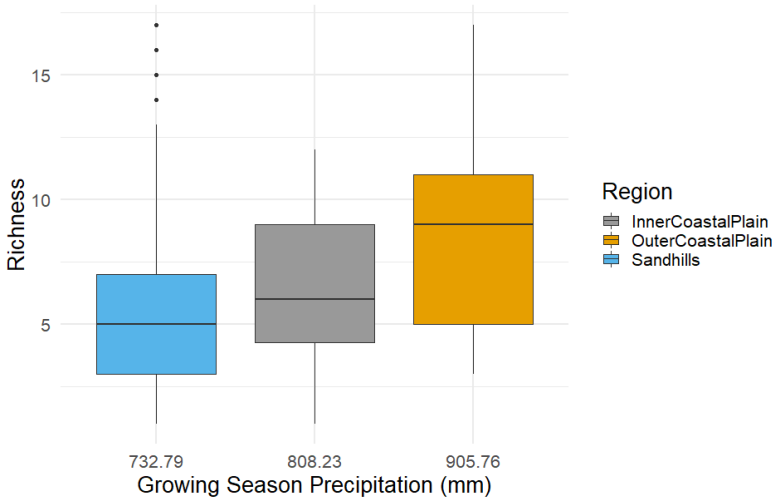


Figure 9. Species Richness as a Function of Ecological Region of North Carolina. The Sandhills (blue), Inner Coastal Plain (grey), and Outer Coastal Plain (gold) Vary in Total Growing Season Precipitation (mm), and Therefore Precipitation May Be a Significant Contributor to Observed Differences in Biodiversity.

Table 2. Calculated Mean Metrics at a $1m^2$ Spatial Scale for Each Study Plot.

Plot Code	Mean Richness	Mean Diversity	Mean Evenness	Mean Dominance	Mean Relative Wiregrass Cover	Mean ANPP
SG1	9.08	4.36	0.488	22.00	30.95	109.91
SG2	11.76	6.46	0.522	23.32	24.47	135.67
Sgpe	4.92	2.59	0.518	23.88	59.71	125.26
WEWO	3.44	2.30	0.584	23.08	37.37	63.76
CFP1	4.72	2.18	0.398	35.52	64.85	159.73
CFP2	3.84	1.85	0.411	35.88	71.60	147.06
CFP3	2.00	1.37	0.399	17.52	85.46	86.21
CACR1	4.56	3.02	0.634	19.88	35.02	120.82
CACR2	6.20	3.76	0.601	21.16	32.99	149.02
CACR3	4.08	2.67	0.580	26.28	38.67	147.44
BLSF1	7.64	3.91	0.469	32.84	36.09	66.72
BLSF2	5.60	3.34	0.478	30.00	28.41	65.76
CNF1	11.30	5.23	0.459	35.39	32.33	164.41
CNF2	4.48	3.27	0.699	23.64	34.29	171.48
CNF3	10.64	6.10	0.555	30.12	15.05	258.03

Table 3. Calculated Total Metrics at a 25m^2 Spatial Scale for Each Study Plot.

Plot Code	Total Richness	Total Diversity	Total Evenness	Total Dominance	Total Relative Wiregrass Cover	Total ANPP
SG1	38	3.30	0.558	15.94	28.05	2747.80
SG2	49	3.58	0.635	20.80	23.80	3391.70
Sgpe	24	2.88	0.674	23.29	55.57	3131.60
WEWO	13	2.15	0.462	22.43	27.85	1593.90
CFP1	27	2.78	0.547	35.63	60.94	3993.30
CFP2	19	2.56	0.651	35.88	70.74	3676.60
CFP3	13	2.31	0.781	17.52	86.90	2155.20
CACR1	27	3.03	0.683	16.13	35.71	3020.40
CACR2	34	3.23	0.615	19.64	31.87	3725.40
CACR3	26	2.94	0.566	23.60	35.85	3686.10
BLSF1	36	3.11	0.468	27.31	32.01	1668.00
BLSF2	25	2.86	0.580	24.78	22.38	1644.00
CNF1	38	3.25	0.663	33.65	31.15	4110.30
CNF2	10	2.16	0.711	19.21	33.60	4287.10
CNF3	36	3.34	0.719	24.08	14.80	6450.80

Mean ANPP varied across plots (63.76 - 258.03g/m^2; Figure 10), as did the contribution of functional groups (graminoid, forb, and woody) in each plot. Across plots, ANPP was primarily composed of graminoids (shown in green), apart from plots located in the Inner Coastal Plain (BLSF1& BLSF2), which had two of the lowest levels of ANPP and were composed of mainly woody species. Additionally, forb ANPP (shown in pink) varied substantially across plots (0.18 – 38.28g/m^2) but was never the dominant functional group. There were significant differences in productivity (mean weight of biomass in each plot) between ecological regions (F = 11.18, p = 0.002; Figure 10). Overall, estimates of mean productivity were highest in the Outer Coastal Plain, closely followed by those in the Sandhills, and were lowest in the Inner Coastal Plain.

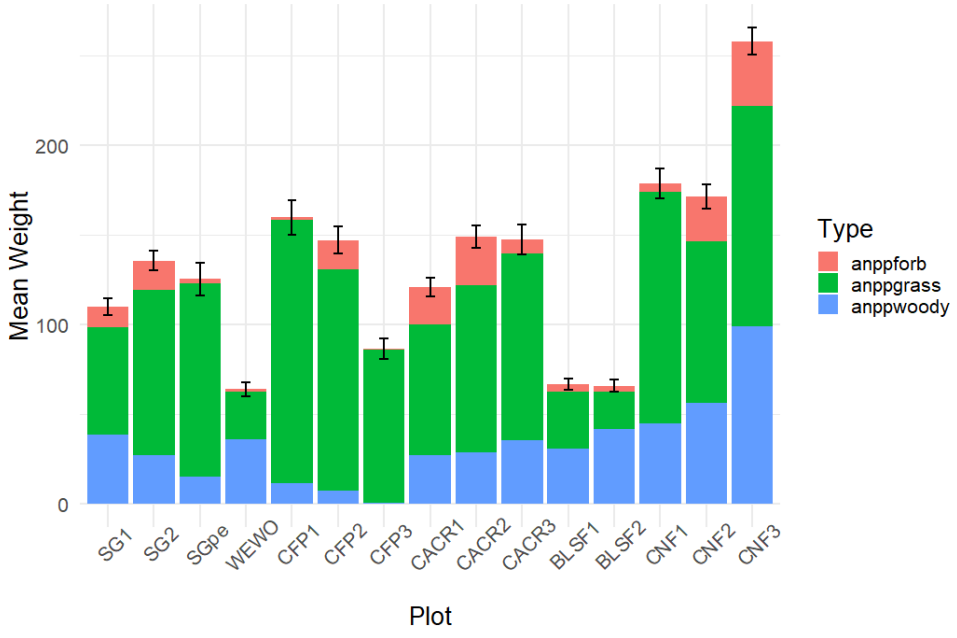


Figure 10. Mean ANPP At Each Study Plot from West to East. Biomass Was Clipped from a 0.1m^2 Area Within Every 1m^2 Species Composition Quadrat. ANPP is Separated by Type, With Forbs Shown in Pink, Graminoids in Green, and Woody Species in Blue. Standard Error Bars Represent How Variable Each Was in Mean ANPP At the Subplot Level.

3.2 Objective 2: Drivers of Variability in Biodiversity, ANPP, and Wiregrass at Small Spatial Scales

Almost all bivariate regression analyses of predictor variables on biodiversity metrics yielded statistically significant relationships. We know that plant community dynamics may be influenced by multiple factors, rather than simply being controlled by one at a time, so we built a multiple regression model, with plot included as a random effect, to account for multiple variables.

With plot included as a random effect in the regression model, there were fewer significant relationships between the predictor variables and biodiversity metrics (Table 4). What stands out from these results is that relative wiregrass cover, and litter cover were consistently found to be correlated with biodiversity metrics and ecosystem process metrics. Relative wiregrass cover had a negative relationship with every metric except for dominance and ANPP where there was a positive relationship, again emphasizing that at high abundances, wiregrass is associated with decreased biodiversity. Additionally, litter cover always had a negative impact on biodiversity.

Table 4. Results of Multiple Regression with a Mixed Effect Model at Small Spatial Scales ($1m^2$).

Metric	Predictor Variable	Estimate	SE	t	P	df
Richness	Light Availability	-0.004	0.005	-0.78	0.436	329
	PC1	-0.022	0.015	-1.497	0.135	338
	Precipitation	0.001	0.001	1.042	0.317	12.2
	Litter Cover	**-0.003**	**<0.001**	**-3.535**	**<0.001**	**337.4**
	ANPP	0.002	0.002	1.457	0.146	328.7
	Relative Wiregrass Cover	**-0.035**	**0.006**	**-6.138**	**<0.001**	**336.0**
	Shrub Stem Numer	0.001	0.009	1.167	0.244	337.9
	Time Since Last Burn	0.157	0.449	0.35	0.733	116.7
	LLP Tree Number	-0.303	0.207	-1.463	0.144	328.6
	Full Model		Conditional R^2: 0.689			
Diversity	Light Availability	0.002	0.003	0.711	0.478	329.7
	PC1	-0.135	0.008	-1.763	0.079	336.7
	Precipitation	0.007	0.005	1.268	0.228	12.63
	Litter Cover	**-0.001**	**<0.001**	**-2.833**	**0.005**	**338.0**
	ANPP	<0.001	<0.001	0.746	0.456	329.4
	Relative Wiregrass Cover	**-0.026**	**0.003**	**-9.003**	**<0.001**	**337.5**
	Shrub Stem Numer	0.005	0.005	1.126	0.261	337.6
	Time Since Last Burn	-0.065	0.199	-0.326	0.75	11.9
	LLP Tree Number	-0.194	0.106	-1.825	0.069	329.2
	Full Model		Conditional R^2: 0.655			
Evenness	Light Availability	<0.001	<0.001	0.483	0.69	337.8
	PC1	0.005	0.011	0.413	0.681	95.7
	Precipitation	<0.001	<0.001	0.535	0.599	18.5
	Litter Cover	<-0.001	<0.001	-0.228	0.82	130
	ANPP	<-0.001	<0.001	-1.508	0.133	337.9
	Relative Wiregrass Cover	**-0.003**	**<0.001**	**-5.725**	**<0.001**	**188.8**
	Shrub Stem Numer	<-0.001	<0.001	-0.929	0.355	133.3
	Time Since Last Burn	**-0.036**	**0.013**	**-2.772**	**0.015**	**14.6**
	LLP Tree Number	0.012	0.018	0.673	0.502	338
	Full Model		Conditional R^2: 0.231			
Dominance	**Light Availability**	**-0.084**	**0.024**	**-3.555**	**<0.001**	**336.8**
	PC1	0.435	0.636	0.684	0.495	194.4
	Precipitation	0.002	0.024	0.083	0.935	18.8
	Litter Cover	-0.006	0.004	-1.603	0.11	238.5
	ANPP	**0.048**	**0.007**	**6.598**	**<0.001**	**336.3**
	Relative Wiregrass Cover	**0.065**	**0.025**	**2.625**	**0.009**	**283.9**
	Shrub Stem Numer	0.013	0.039	0.324	0.746	229.6
	Time Since Last Burn	**3.343**	**0.858**	**3.896**	**0.001**	**15.5**
	LLP Tree Number	1.568	0.952	1.648	0.1	336
	Full Model		Conditional R^2: 0.374			
Relative Wiregrass Cover	Light Availability	0.09	0.05	1.812	0.071	331.4
	PC1	-1.72	1.437	-1.197	0.232	332.6
	Precipitation	-0.058	0.091	-0.632	0.539	12.9
	Litter Cover	-0.007	0.009	-0.835	0.404	337.5
	ANPP	**0.035**	**0.015**	**2.335**	**0.02**	**330.5**
	Shrub Stem Numer	-0.149	0.087	-1.714	0.088	334.3
	Time Since Last Burn	-5.2	3.333	-1.56	0.145	11.9
	LLP Tree Number	0.338	2.013	0.168	0.867	330.6
	Full Model		Conditional R^2: 0.543			
ANPP	Light Availability	-0.314	0.176	-1.783	0.075	338.8
	PC1	4.838	4.527	1.069	0.287	117
	Precipitation	0.15	0.152	0.987	0.335	20.7
	Litter Cover	**-0.094**	**0.027**	**-3.441**	**<0.001**	**155.9**
	Relative Wiregrass Cover	**0.383**	**0.179**	**2.135**	**0.034**	**218.6**
	Shrub Stem Numer	<0.001	0.282	0.001	0.999	157.5
	Time Since Last Burn	-9.261	5.233	-1.77	0.095	16.3
	LLP Tree Number	-10.67	7.128	-1.496	0.135	339
	Full Model		Conditional R^2: 0.247			

3.3 Objective 2: Drivers of Variability in Biodiversity, ANPP, and Wiregrass at Local Spatial Scales

Bivariate regression analyses of mean predictor variables on mean biodiversity metrics yielded few significant relationships (Table 5). Mean relative wiregrass cover was found to be significantly correlated with mean richness ($P = 0.006$), mean diversity ($P < 0.001$), and mean evenness ($P = 0.022$). LLP tree number and the number of shrub stems also had significant relationships with our mean biodiversity metrics, and mean ANPP was significantly influenced by abiotic predictors (light availability, soil nutrients, and time since burn), as was expected.

Bivariate regression analyses of predictor variables on total biodiversity metrics also yielded few significant relationships (Table 6). For these analyses at the plot level, predictor variables were mean light availability, mean PC1, precipitation, time since last burn, total litter cover, total ANPP, total relative wiregrass cover, total shrub stem number, and total number of LLP trees at the $25m^2$ spatial scale. Again, at this local scale, total relative wiregrass cover was found to have marginally significant relationships with total richness ($P = 0.053$) and total diversity (0.057). The number of LLP trees in a plot was found to be negatively correlated with both total richness ($P = 0.001$) and total diversity ($P < 0.001$) and, time since last burn was correlated with total plot evenness ($P=0.025$), and light availability was correlated with total ANPP ($P=0.002$).

Table 5. Bivariate Regression Analyses on Mean Biodiversity Metrics at a Local Spatial Scale ($1m^2$).

Metric	Predictor	Estimate	SE	t	P	R^2	F	df
Mean Richness	Light Availability	-0.092	0.068	-1.365	0.197	0.134	1.864	(1, 12)
	PC1	0.666	0.538	1.238	0.238	0.106	1.533	(1, 13)
	Precipitation	0.019	0.011	1.784	0.098	0.197	3.182	(1, 13)
	Litter Cover	-0.005	0.006	-0.817	0.429	0.049	0.667	(1, 13)
	ANPP	0.024	0.015	1.542	0.147	0.155	2.379	(1, 13)
	Relative Wiregrass Cover	**-0.106**	**0.032**	**-3.282**	**0.006**	**0.453**	**10.77**	**(1, 13)**
	Shrub Stem Number	-0.143	0.167	-0.86	0.405	0.054	0.74	(1, 13)
	Time Since Last Burn	0.264	0.5	0.527	0.607	0.021	0.277	(1, 13)
	LLP Tree Number	**-0.307**	**0.134**	**-2.289**	**0.04**	**0.287**	**5.237**	**(1, 13)**
Mean Diversity	Light Availability	-0.46	0.031	-1.466	0.169	0.152	2.15	(1, 12)
	PC1	0.382	0.237	0.618	0.13	0.168	2.619	(1, 13)
	Precipitation	0.01	0.005	2.008	0.0659	0.237	4.032	(1, 13)
	Litter Cover	-0.002	0.003	-0.572	0.577	0.025	0.327	(1, 13)
	ANPP	0.013	0.007	1.769	0.1	0.194	3.13	(1, 13)
	Relative Wiregrass Cover	**-0.06**	**0.013**	**-4.7**	**<0.001**	**0.63**	**22.09**	**(1, 13)**
	Shrub Stem Number	-0.037	0.08	-0.471	0.646	0.037	0.494	(1, 13)
	Time Since Last Burn	0.06	0.247	0.241	0.813	0.004	0.058	(1, 13)
	LLP Tree Number	-0.11	0.072	-1.52	0.153	0.151	2.309	(1, 13)
Mean Evenness	Light Availability	-0.0005	0.002	-0.228	0.824	0.004	0.052	(1, 12)
	PC1	0.026	0.014	1.909	0.079	0.219	3.643	(1, 13)
	Precipitation	0.0002	0.0003	0.588	0.566	0.026	0.346	(1, 13)
	Litter Cover	0.0002	0.0002	1.213	0.247	0.102	1.471	(1, 13)
	ANPP	<0.001	<0.001	0.067	0.948	0.0003	0.004	(1, 13)
	Relative Wiregrass Cover	**-0.003**	**0.001**	**-2.607**	**0.022**	**0.343**	**6.796**	**(1, 13)**
	Shrub Stem Number	**0.01**	**0.004**	**2.598**	**0.022**	**0.342**	**3.127**	**(1, 13)**
	Time Since Last Burn	-0.019	0.013	-1.528	0.151	0.152	2.333	(1, 13)
	LLP Tree Number	0.007	0.004	1.776	0.099	0.195	3.154	(1, 13)
Mean Dominance	Light Availability	0.056	0.155	0.363	0.723	0.011	0.132	(1, 12)
	PC1	-1.076	1.093	-0.984	0.343	0.069	0.969	(1, 13)
	Precipitation	0.032	0.022	1.449	0.171	0.139	2.1	(1, 13)
	Litter Cover	-0.009	0.012	-0.729	0.479	0.039	0.532	(1, 13)
	ANPP	0.031	0.032	0.951	0.359	0.065	0.905	(1, 13)
	Relative Wiregrass Cover	0.003	0.087	0.038	0.97	0.0001	0.001	(1, 13)
	Shrub Stem Number	-0.403	0.322	-1.251	0.233	0.107	1.565	(1, 13)
	Time Since Last Burn	1.565	0.908	1.724	0.108	0.186	2.97	(1, 13)
	LLP Tree Number	-0.241	0.31	-0.777	0.451	0.044	0.604	(1, 13)
Mean Relative Wiregrass Cover	Light Availability	0.233	0.458	0.509	0.62	0.021	0.259	(1, 12)
	PC1	-6.169	3.17	-1.946	0.074	0.226	3.788	(1, 13)
	Precipitation	-0.127	0.067	-1.891	0.081	0.216	3.575	(1, 13)
	Litter Cover	-0.024	0.038	-0.637	0.535	0.03	0.405	(1, 13)
	ANPP	-0.094	0.103	-0.913	0.378	0.06	0.833	(1, 13)
	Shrub Stem Number	-0.403	0.322	-1.251	0.233	0.107	1.565	(1, 13)
	Time Since Last Burn	1.565	0.908	1.724	0.108	0.186	2.97	(1, 13)
	LLP Tree Number	-0.241	0.31	-0.777	0.451	0.044	0.604	(1, 13)
Mean ANPP	**Light Availability**	**-2.46**	**0.624**	**-3.941**	**0.002**	**0.564**	**15.53**	**(1, 12)**
	PC1	**17.746**	**7.225**	**2.456**	**0.03**	**0.317**	**6.032**	**(1, 13)**
	Precipitation	0.347	0.172	2.012	0.066	0.237	4.047	(1, 13)
	Litter Cover	-0.138	0.094	-1.467	0.166	0.142	2.152	(1, 13)
	Relative Wiregrass Cover	-0.641	0.702	-0.913	0.378	0.06	0.833	(1, 13)
	Shrub Stem Number	-0.18	2.831	-0.064	0.95	0.0003	0.004	(1, 13)
	Time Since Last Burn	**-16.736**	**6.951**	**-2.408**	**0.032**	**0.308**	**5.796**	**(1, 13)**
	LLP Tree Number	-0.634	2.623	-0.242	0.813	0.005	0.059	(1, 13)

Table 6. Bivariate Regression Analyses on Total Biodiversity Metrics at a Local Spatial Scale ($25m^2$).

Metric	Predictor	Estimate	SE	t	P	R^2	F	df
Total Richness	Light Availability	-0.378	0.254	-1.486	0.163	0.156	2.21	(1, 12)
	PC1	1.151	2.01	0.572	0.577	0.025	0.328	(1, 13)
	Precipitation	0.008	0.043	0.198	0.846	0.003	0.039	(1, 13)
	Litter Cover	-0.011	0.022	-0.501	0.624	0.019	0.251	(1, 13)
	ANPP	0.05	0.058	0.858	0.406	0.054	0.767	(1, 13)
	Relative Wiregrass Cover	**-0.28**	**0.131**	**-2.132**	**0.053**	**0.26**	**4.545**	**(1, 13)**
	Shrub Stem Number	<0.001	<0.001	0.044	0.965	<0.001	0.002	(1, 13)
	Time Since Last Burn	1.351	1.769	0.763	0.459	0.043	0.583	(1, 13)
	LLP Tree Number	**-1.542**	**0.375**	**-4.111**	**0.001**	**0.565**	**16.9**	**(1, 13)**
Total Diversity	Light Availability	-0.016	0.01	-1.609	0.134	0.177	2.587	(1, 12)
	PC1	0.063	0.079	0.789	0.444	0.046	0.623	(1, 13)
	Precipitation	0.0003	0.002	0.183	0.858	0.003	0.033	(1, 13)
	Litter Cover	<0.001	<0.001	-0.56	0.585	0.024	0.313	(1, 13)
	ANPP	0.003	0.002	1.144	0.273	0.092	1.31	(1, 13)
	Relative Wiregrass Cover	**-0.011**	**0.005**	**-2.086**	**0.057**	**0.251**	**4.349**	**(1, 13)**
	Shrub Stem Number	<0.001	<0.001	0.399	0.697	0.012	0.159	(1, 13)
	Time Since Last Burn	0.033	0.072	0.466	0.649	0.016	0.217	(1, 13)
	LLP Tree Number	**-0.066**	**0.014**	**-4.799**	**<0.001**	**0.639**	**23.03**	**(1, 13)**
Total Evenness	Light Availability	-0.003	0.002	-1.475	0.166	0.153	2.175	(1, 12)
	PC1	0.02	0.016	1.286	0.221	0.113	1.654	(1, 13)
	Precipitation	0.0003	0.0003	1.047	0.314	0.078	1.096	(1, 13)
	Litter Cover	<0.001	<0.001	-1.312	0.212	0.117	1.721	(1, 13)
	ANPP	<0.001	<0.001	1.997	0.067	0.235	3.99	(1, 13)
	Relative Wiregrass Cover	0.002	0.001	1.312	0.212	0.117	1.721	(1, 13)
	Shrub Stem Number	<0.001	<0.001	-0.672	0.513	0.034	0.451	(1, 13)
	Time Since Last Burn	**-0.031**	**0.012**	**-2.535**	**0.025**	**0.331**	**6.425**	**(1, 13)**
	LLP Tree Number	<0.001	0.005	-0.118	0.908	0.001	0.014	(1, 13)
Total Dominance	Light Availability	0.013	0.169	0.077	0.9397	0.0005	0.006	(1, 12)
	PC1	-1.639	1.13	-1.45	0.171	0.139	2.103	(1, 13)
	Precipitation	0.016	0.025	0.652	0.526	0.032	0.425	(1, 13)
	Litter Cover	-0.009	0.013	-0.676	0.511	0.034	0.457	(1, 13)
	ANPP	0.026	0.035	0.749	0.467	0.041	0.561	(1, 13)
	Relative Wiregrass Cover	0.078	0.089	0.876	0.397	0.056	0.767	(1, 13)
	Shrub Stem Number	-0.008	0.004	-1.972	0.07	0.23	3.887	(1, 13)
	Time Since Last Burn	1.075	1.041	1.033	0.32	0.076	1.067	(1, 13)
	LLP Tree Number	-0.188	0.336	-0.56	0.585	0.024	0.313	(1, 13)
Total Relative Wiregrass Cover	Light Availability	0.073	0.484	0.152	0.882	0.002	0.023	(1, 12)
	PC1	-5.329	3.399	-1.568	0.141	0.159	2.458	(1, 13)
	Precipitation	-0.12	0.07	-1.704	0.112	0.183	2.904	(1, 13)
	Litter Cover	-0.03	0.039	-0.796	0.44	0.046	0.633	(1, 13)
	ANPP	-0.065	0.108	-0.607	0.554	0.028	0.369	(1, 13)
	Shrub Stem Number	-0.013	0.014	-0.882	0.394	0.056	0.778	(1, 13)
	Time Since Last Burn	-2.275	3.233	-0.704	0.494	0.037	0.495	(1, 13)
	LLP Tree Number	0.032	1.036	0.031	0.976	<0.001	<0.001	(1, 13)
Total ANPP	**Light Availability**	**-2.46**	**0.624**	**-3.941**	**0.002**	**0.564**	**15.53**	**(1, 12)**
	PC1	17.746	7.225	2.456	0.029	0.317	6.032	(1, 13)
	Precipitation	0.347	0.172	2.012	0.066	0.237	4.047	(1, 13)
	Litter Cover	-0.138	0.094	-1.467	0.166	0.142	2.152	(1, 13)
	Relative Wiregrass Cover	-0.421	0.694	-0.607	0.554	0.028	0.369	(1, 13)
	Shrub Stem Number	-0.003	0.038	-0.072	0.944	<0.001	0.005	(1, 13)
	Time Since Last Burn	**-16.736**	**6.951**	**-2.408**	**0.032**	**0.308**	**5.796**	**(1, 13)**
	LLP Tree Number	-0.634	2.623	-0.242	0.813	0.005	0.059	(1, 13)

After calculating the CV, or heterogeneity, of ANPP, relative wiregrass cover, and richness, those values were then used in regression analyses to identify what predictor variables may be influencing their variability. When looking at the heterogeneity of ANPP across my study, we found that the CV of ANPP was significantly correlated with the number of shrub stems in a subplot. The heterogeneity of relative wiregrass cover was significantly correlated with light availability and time since last burn. Finally, the heterogeneity of richness was significantly correlated with PC1 and ANPP (Table 8).

Table 7. Regression Analyses of Predictor Variables on the Coefficient of Variation (CV) of ANPP, Relative Wiregrass Cover, and Richness.

Metric	Predictor Variable	Estimate	SE	t	P	R^2	F	DF
CV of ANPP	Light Availability	0.583	0.31	1.88	0.085	0.0227	3.533	(1, 12)
	PC1	-2.358	2.716	-0.868	0.401	0.055	0.754	(1, 13)
	Precipitation	-0.068	0.06	-1.127	0.28	0.089	1.269	(1, 13)
	Litter Cover	-0.005	0.032	-0.146	0.886	0.002	0.021	(1, 13)
	Relative Wiregrass Cover	0.198	0.225	0.881	0.394	0.056	0.777	(1, 13)
	Shrub Stem Number	**1.89**	**0.688**	**2.744**	**0.017**	**0.367**	**7.529**	**(1, 13)**
	Time Since Last Burn	0.619	2.666	0.232	0.82	0.004	0.054	(1, 13)
	LLP Tree Number	0.322	0.835	0.386	0.706	0.011	0.149	(1, 13)
CV of Relative Wiregrass Cover	**Light Availability**	**1.092**	**0.449**	**2.431**	**0.032**	**0.33**	**5.91**	**(1, 12)**
	PC1	-3.819	3.524	-1.084	0.298	0.083	1.175	(1, 13)
	Precipitation	0.008	0.083	0.092	0.928	<0.001	0.008	(1, 13)
	Litter Cover	0.051	0.04	1.288	0.22	0.11	1.659	(1, 13)
	ANPP	-0.189	0.104	-1.807	0.094	0.201	3.265	(1, 13)
	Shrub Stem Number	0.485	1.13	0.429	0.675	0.014	0.184	(1, 13)
	Time Since Last Burn	**8.346**	**2.649**	**3.151**	**0.008**	**0.433**	**9.927**	**(1, 13)**
	LLP Tree Number	-0.081	1.106	-0.073	0.943	<0.001	0.005	(1, 13)
CV of Richness	Light Availability	0.323	0.163	1.989	0.07	0.248	3.955	(1, 12)
	PC1	**-3.309**	**1.149**	**-2.88**	**0.013**	**0.39**	**8.296**	**(1, 13)**
	Precipitation	0.049	0.03	-1.629	0.127	0.17	2.653	(1, 13)
	Litter Cover	0.023	0.016	1.448	0.171	0.139	2.098	(1, 13)
	ANPP	**-0.115**	**0.034**	**-3.38**	**0.005**	**0.468**	**11.43**	**(1, 13)**
	Relative Wiregrass Cover	0.18	0.111	1.619	0.13	0.168	2.62	(1, 13)
	Shrub Stem Number	-0.11	0.454	-242	0.812	0.005	0.059	(1, 13)
	Time Since Last Burn	1.468	1.346	1.091	0.295	0.084	1.19	(1, 13)
	LLP Tree Number	0.213	0.438	0.486	0.635	0.018	0.236	(1, 13)

3.4 Objective 2: Productivity and Biodiversity

Polynomial mixed effect regression analysis showed that the relationship between ANPP and biodiversity, specifically richness, was significant (first order: P = 0.002, t = 3.136, df = 359.6; second order: P = 0.005, t = -2.831, df = 357.8; model conditional R^2 = 0.65). When we fit a polynomial regression with regression lines for each study plot as well as a pooled line representing overall effect, we see a unimodal trend in the relationship between ANPP and species richness, with richness peaking at 274.3g/m^2 (Figure 11).

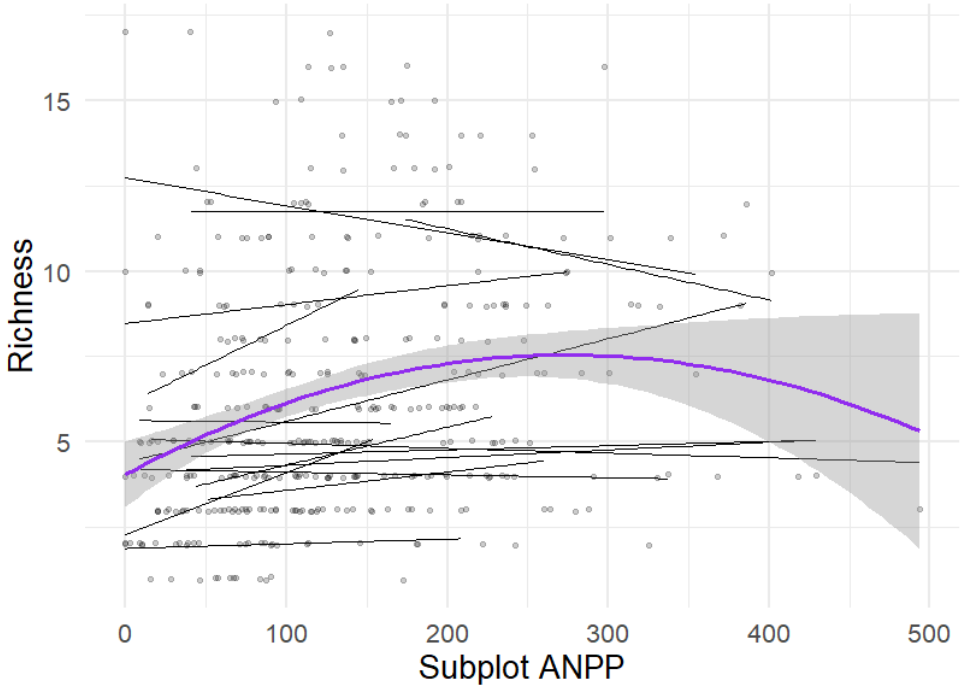


Figure 11. Subplot Richness as a Function of ANPP. Thin Black Lines Represent the Trend for Each Plot and the Purple Line Represents the Overall Trend.

3.5 Objective 2: Drivers of Wiregrass and the Effects on Biodiversity

When comparing all subplots where *A. stricta was* present (regardless of the abundance) to subplots where the grass species was not present, there was a significant difference in mean richness ($P < 0.001$). Mean richness was higher in subplots containing wiregrass ($S = 8.59$) than those where wiregrass was absent ($S = 7.24$, Figure 12a). There was also a significant difference ($P < 0.001$) when looking at mean diversity between subplots where wiregrass was present/absent. Mean diversity was higher in subplots where wiregrass was present ($div = 4.56$) than those where it was absent ($div = 3.93$, Figure 12b). This suggests that the mere presence of *A. stricta* in the understory of LLP savannas facilitates biodiversity.

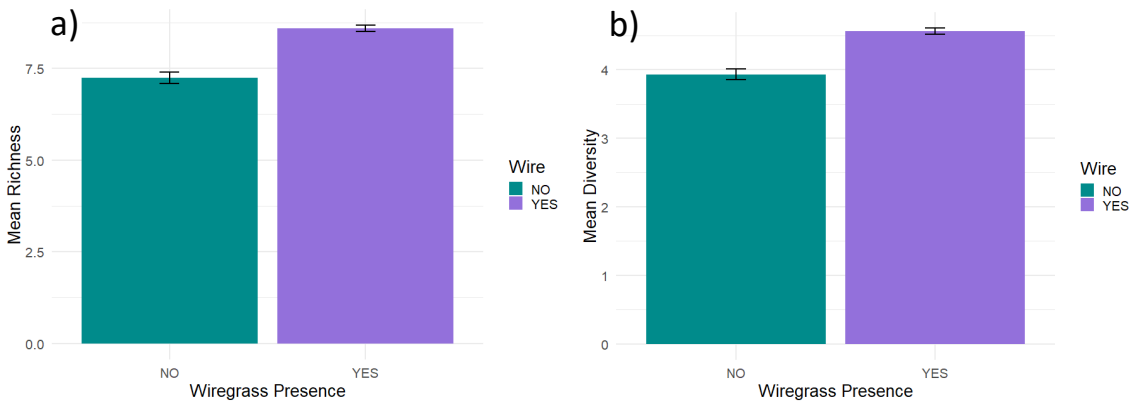


Figure 12. Mean Richness (a) and Mean Diversity (b) in Subplots Without Wiregrass Present (teal) and in Subplots Containing Wiregrass (purple).

To further investigate the influence of wiregrass on biodiversity, polynomial mixed effect regression of relative wiregrass cover on richness at a small scale was performed (first order: $P = 0.055$, $t = 1.922$, $df = 361.8$; second order: $P < 0.001$, $t = -4.642$, $df = 363.3$; model conditional $R^2 = 0.66$). Figure 13 shows subplot richness as

a function of the relative cover of wiregrass with regression lines fit for each study plot, with one pooled line that represents the overall relationship between relative wiregrass cover and richness. As the relative wiregrass cover in a subplot increases, richness declines. This result indicates that while the presence of wiregrass is important for maintaining biodiversity, a high relative cover (abundance) of wiregrass negatively impacts species richness, likely due to its dominance and resource acquisition when at higher abundances.

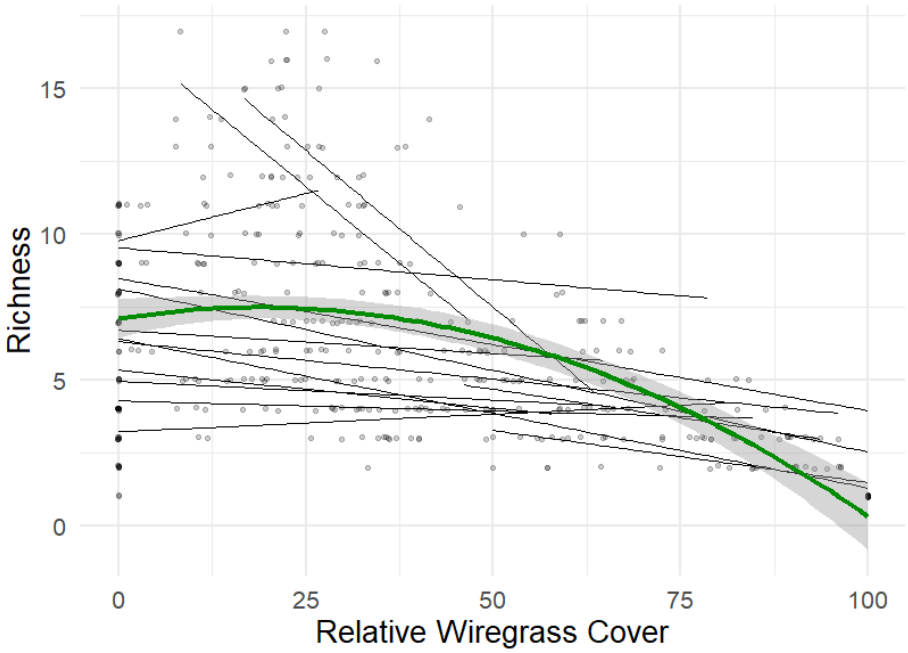


Figure 13. Subplot Richness as a Function of Relative Wiregrass Cover. Thin Black Lines Represent the Trend for Each Plot and the Green Line Represents Overall Trend.

To explore if there is a relative cover of wiregrass that is optimal for maintaining biodiversity, we again plotted richness against relative wiregrass cover and then found the global maximum of the pooled, green curve. Figure 14 shows the relationship

between relative wiregrass cover and richness of just graminoid and forb species. When excluding woody and tree species, the ideal relative wiregrass cover at small scales was 16.42% (Figure 14).

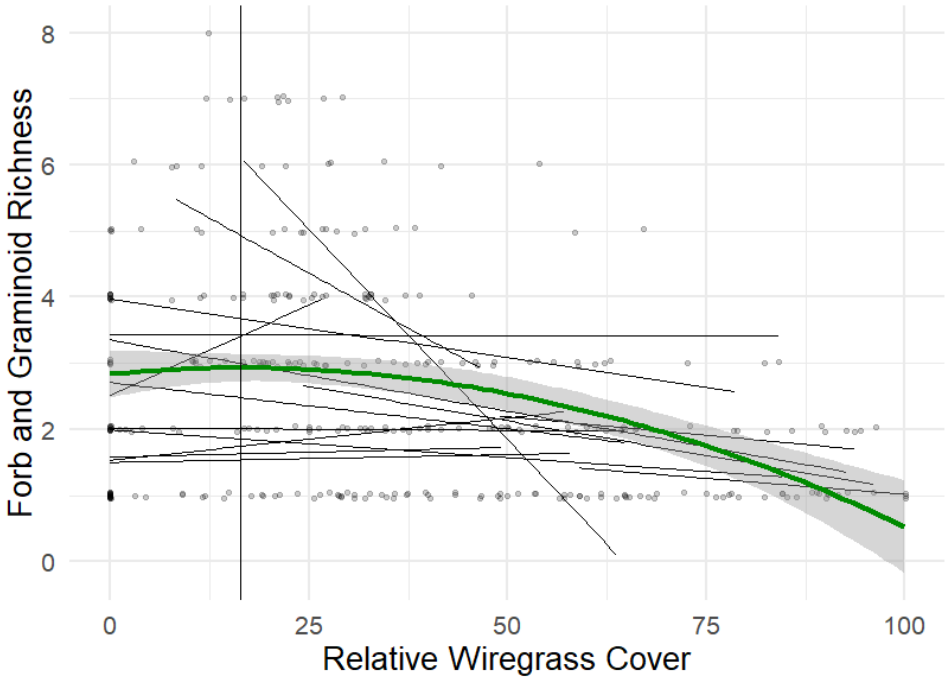


Figure 14. Regression of Relative Wiregrass Cover on Total Richness of Graminoid and Forb Species. The Vertical Black Line Represent the Global Maximum, or Peak of the Regression Curve.

Multiple regression analyses of predictor variables on relative wiregrass cover, shown in Table 9, showed that wiregrass is positively influenced by light availability ($P < 0.001$) and negatively influenced by precipitation ($P < 0.001$), litter cover ($P < 0.001$), the time since last burn ($P < 0.001$), and the number of shrub stems ($P < 0.001$). Based on these results, we can say that the optimal environment for wiregrass is where there is plenty of light reaching the understory, enough precipitation for optimal growth but not as much as is seen along the coastal plain, frequent fire, few shrubs, and low litter cover.

Table 8. Multiple Regression Analysis of Predictor Variables on Relative Wiregrass Cover.

Model: $R^2 = 0.256$, $F = 15.94$, $df = (8, 339)$, $P < 0.001$

Metric	Predictor Variable	Estimate	SE	t	P
Relative Wiregrass Cover	**Light Availability**	**0.158**	**0.06**	**2.668**	**0.008**
	PC1	-2.005	1.245	-1.61	0.108
	Precipitation	**-0.088**	**0.035**	**-2.526**	**0.012**
	Litter Cover	**-0.031**	**0.008**	**-3.919**	**< 0.001**
	ANPP	0.033	0.018	1.821	0.07
	Shrub Stem Number	**-0.5**	**0.077**	**-6.472**	**< 0.001**
	Time Since Last Burn	**-6.258**	**1.107**	**-5.656**	**< 0.001**
	LLP Tree Number	-0.26	2.426	-0.107	0.915

3.6 Discussion

This study conducted in LLP-wiregrass understory communities occurred within three ecoregions which differed in their geography and environmental conditions. Sites in the Outer Coastal plain received more precipitation during the growing season, occurred on poorly-drained soils, and were lower in elevation. In contrast, sites in the Sandhills received less precipitation, and occurred primarily on uplands and on well-drained soils, with characteristics of sites in the Inner Coastal Plain falling in the middle of the previous two ecoregions.

3.6.1 Heterogeneity

Along with geographical variation, this study found considerable variation in biodiversity metrics, ANPP, and relative wiregrass cover across plots in North Carolina. The heterogeneity (CV) of these response variables across my study was only explained by a few of the predictor variables. With an increase in the number of shrub stems in a subplot, we found an increase in the variability of ANPP, indicating that the understories

with variable distributions of biomass may be influenced by small understory shrubs that utilize the resources (*i.e.* water, nutrients, sunlight) that other understory plants need in order to produce more aboveground biomass. An increase in light availability and time since last burn contributed to greater heterogeneity of wiregrass cover, meaning that understories with patchy wiregrass distributions are most likely the result of long fire return intervals and little light availability. Finally, an increase in PC1 and ANPP contributed to less heterogeneity of species richness, meaning that understories with consistent levels of richness are most likely the result of even distributions of aboveground biomass and soil nutrient levels. These results highlight the importance of preserving and restoring the diverse and variable LLP savanna ecosystem, especially in NC where this study found high biodiversity and wide variability across the state.

3.6.2 Drivers of Biodiversity

The linear mixed effect model with all predictor variables included, showed that some of the predictors (*i.e.* shrub stem number, LLP tree number, precipitation, and time since last burn) no longer had significant relationships with biodiversity metrics. This, however, does not mean that there is not a relationship, just that in the presence of predictors like relative wiregrass cover and litter cover, those other predictors were not as important in influencing our biodiversity metrics. Wiregrass cover had a significantly negative relationship in multiple regression models of biodiversity metrics. This means that although the presence of wiregrass is a positive driver of biodiversity as described earlier, a high cover (abundance) of wiregrass can have a negative effect on biodiversity.

As demonstrated by this and other studies, biodiversity in LLP savanna understories must be analyzed at multiple spatial scales to achieve the full picture of what is driving biodiversity within ecosystems. Our regression analyses at the subplot ($1m^2$) and plot ($25m^2$) level had a few similarities but many different combinations of drivers at both spatial scales. On a small spatial scale, biodiversity of plant communities in North Carolina LLP savannas are mainly driven by litter cover and wiregrass cover. Looking specifically at litter cover (*i.e.* weight of LLP needles covering the soil surface) at small and local spatial scales, we see that as litter increases, biodiversity decreases, emphasizing the importance of a sparse overstory and maintaining regular fire disturbances that will keep the soil surface clear, allowing understory plant species room and resources in which to flourish. Manual removal of litter cover (pine-straw raking) is not recommended as this will likely disturb the understory plant community and have a negative effect on biodiversity. Also, at both spatial scales, relative wiregrass cover had a consistent negative relationship with metrics of biodiversity. In fact, relative wiregrass cover was the only major biodiversity driver at both small and local scales, emphasizing its influence on the understory plant community.

3.6.3 Wiregrass and Biodiversity

Subplots containing wiregrass were on average more biodiverse than subplots lacking wiregrass, but what this study has shown is that too much wiregrass cover can have a negative effect on biodiversity. Other studies in LLP-wiregrass communities have suggested that managers should encourage the dominance (abundance) of wiregrass, because it and other bunchgrass species alike, are noncompetitive grass species (Roth et

al. 2008, Myers and Harms 2009), and would provide fine fuel for fire, thereby increasing richness and diversity (Kirkman et al. 2016). Although wiregrass is an ideal grass species for carrying fire across the landscape, its dominance in the understory is associated with lower levels of richness and diversity, as shown in this study. Therefore, there must be some intermediate abundance of wiregrass at small spatial scales that is ideal for maintaining and enhancing biodiversity. This study proposes that there is indeed an ideal relative cover of wiregrass at a $1m^2$ spatial scale that would enhance and maintain biodiversity of LLP-wiregrass community understories. Depending on what plant functional groups are present in the understory, the ideal relative cover varies. In LLP understory plant communities, the grass and forb species are what contribute to the high diversity of the understory, and so when addressing the richness of just graminoid and forb species, the ideal cover of wiregrass at a small scale is ~16%. LLP-wiregrass savanna land managers could implement these suggested relative percent covers in their restoration plans and potentially increase the biodiversity in their stands.

3.6.4 Productivity and Biodiversity

Studies of other grassland ecosystems in North America have reported a decrease in species richness with an increase in biomass (Barnes et al. 1983, Gibson and Hulbert 1987), and a study conducted in LLP-*A. stricta* communities reported that richness peaked at a productivity measurement of around $280g/m^2$, thereby showing a unimodal relationship (Walker and Peet 1984). This study also found a unimodal productivity-biodiversity relationship, with richness peaking at ~$275g/m^2$. The unimodal direction of this productivity-biodiversity relationship may be particular to LLP-*A. stricta*

communities, as studies in LLP-*A. beyrichiana* communities have reported a positive relationship (Kirkman et al. 2001).

3.7 Conclusion

Although the ideal percentages of wiregrass suggested here may be useful, experimental studies are needed in which wiregrass abundance is manipulated so that we can determine with more power, the wiregrass abundance that gives rise to greater biodiversity. More research is needed on the dynamics and influence of wiregrass on biodiversity in order to make confident recommendations to LLP savanna land managers for restoration purposes. With sound recommendations, the management and health of these lands will improve. This would increase the potential for LLP savannas to expand throughout the Coastal Plain and back into the historical range, becoming the dominant ecosystem type again.

This study identifies potential drivers of biodiversity across our study sites; however, it is important to recognize that this only describes the dynamics of the understory at one time point. To understand the absolute dynamics of a plant community, drivers of biodiversity must be studied over extended periods as many characteristics of these communities are developed slowly over time. Annual plant community changes may stem from populations of species changing in response to relatively short-term environmental changes, but secondary succession, or the change in community composition following a disturbance event, has a longer temporal pattern. Therefore, long-term studies are needed to gain a better grasp on the dynamics of an understory plant community disturbed by fire on a regular basis (every 2-3 years).

Overall, this thesis provides a baseline of understory biodiversity and plant community dynamics for LLP savannas in NC as well as a broad understanding of the drivers that control the variability seen at multiple spatial scales. These 15 sites showed substantial variation in all biodiversity metrics. For example, small scale ($1m^2$) richness varied from 2 species to 11 species. While the biodiversity of the understory was impacted by broad site-level changes in abiotic drivers across the ecoregions, such as soil moisture availability, almost all measures of biodiversity were affected by wiregrass cover, ANPP, and biomass of pine needle litter. This suggests that while resource availability is important for establishing environmental filters and regional diversity patterns, small ($1m^2$) and local ($25m^2$) scale biodiversity are controlled strongly by the dominant species. Pine needle litter biomass is a direct result of the dominant overstory species, the longleaf pine, and both wiregrass cover and ANPP are a result of the dominant understory species, wiregrass.

Relative wiregrass cover ranged from 0% to 100% and ecosystem function, measured here as ANPP, ranged from $0g/m^2$ to $493.8g/m^2$. This large variation contributed substantially to the variation seen in biodiversity. These findings suggest that managing for wiregrass cover is an important component for restoring LLP understories to high levels of diversity. Wiregrass must be present in the understory; however, the level of wiregrass must be kept relatively low (~16%) in order to ensure space and resource availability for other grass species and forbs which contribute greatly to biodiversity. While more experimental evidence is required to determine direct causation, managers can potentially use wiregrass presence and abundance as a predictor of

biodiversity dynamics on their land. This will lead to more frequent understory monitoring as managers will be able to eliminate the exhaustive and high-skill requiring, biodiversity surveys.

The majority of LLP savanna is found on private land. Range-wide, 62% of LLP-dominated stands are owned by nonindustrial private landowners (Oswalt et al. 2012). Importantly, some of those private landowners restore LLP on a small scale. This may be for many different reasons, including that they only own a small tract of land, they don't have the money to restore or are not educated on cost-share programs for restoration, or they are only interested in restoring a portion of their land back to LLP. Therefore, information at smaller spatial scales – like that provided here – while important to consider when restoring large areas, is crucial for the private landowners desiring to reach certain biodiversity targets on a small scale. This study shows that managing longleaf pine trees is not enough to bring back the biodiversity of the understory. Instead, land managers must focus on the dominant understory species as well, as it controls the resources left for the other species. Wiregrass must be present in order to ensure adequate fire; however, too much, and other species cannot thrive. Here I provide guidance on what is an ideal wiregrass cover when trying to enhance the biodiversity of the understory. LLP savannas are so much more than the LLP tree that dominates the skyline and understanding the drivers of the understory biodiversity will aid in the restoration of an essential component of this critically threatened ecosystem.

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Appendix A.

Descriptive Tables

Table A1. Regional Average Low and High Temperatures (°C) and Total Precipitation (mm) Over the Growing Season (GS).

Region	Average Low Temperature (°C)	Average High Temperature (°C)	Total Precipitation (mm)
Sandhills	15.63	27.94	732.79
Inner Coastal Plain	15.48	28.09	808.23
Outer Coastal Plain	15.95	28.26	905.76

Table A2. Region, Soil Taxonomy, Community Vegetation Classification, and Elevation for Each Study Plot.

Plot Code	Plot Location	Plot Region	Soil Taxonomy	Vegetation Classification	Elevation (m.a.s.l.)
SG1	Sandhill Gamelands	Sandhills	Wakulla and Candor soils	Xeric Sandhill Scrub (Turkey Oak Variant)	129.4
SG2	Sandhill Gamelands	Sandhills	Ailey loamy sand	Pine/Scrub Oak Sandhill (Blackjack Subtype)	120.4
Sgpe	Sandhill Gamelands	Sandhills	Ailey loamy sand	Pine/Scrub Oak Sandhill (Blackjack Subtype)	126.23
WEWO	Weymouth Woods	Sandhills	Ailey loamy sand	Xeric Sandhill Scrub (Typic Subtype)	130.75
CFP1	Calloway Forest Preserve	Sandhills	Candor sand	Xeric Sandhill Scrub (Typic Subtype)	95.77
CFP2	Calloway Forest Preserve	Sandhills	Candor sand	Xeric Sandhill Scrub (Typic Subtype)	119.65
CFP3	Calloway Forest Preserve	Sandhills	Candor sand	Xeric Sandhill Scrub (Typic Subtype)	106.07
CACR1	Carvers Creek State Park	Sandhills	Blaney loamy sand	Pine/Scrub Oak Sandhill (Mixed Oak Subtype)	75.23
CACR2	Carvers Creek State Park	Sandhills	Blaney loamy sand	Pine/Scrub Oak Sandhill (Mixed Oak Subtype)	57.68
CACR3	Carvers Creek State Park	Sandhills	Blaney loamy sand	Pine/Scrub Oak Sandhill (Mixed Oak Subtype)	58.91
BLSF1	Bladen Lakes State Forest	Inner Coastal Plain	Leon sand	Pine/Scrub Oak Sandhill (Mixed Oak Subtype)	27.24
BLSF2	Bladen Lakes State Forest	Inner Coastal Plain	Leon sand	Pine/Scrub Oak Sandhill (Mixed Oak Subtype)	27.5
CNF1	Croatan National Forest	Outer Coastal Plain	Mandarin sand	Mesic Pine Savanna (Coastal Plain Subtype)	11.37
CNF2	Croatan National Forest	Outer Coastal Plain	Murville mucky sand	Mesic Pine Savanna (Coastal Plain Subtype)	10.51
CNF3	Croatan National Forest	Outer Coastal Plain	Onslow loamy sand	Mesic Pine Savanna (Coastal Plain Subtype)	9.03

Appendix B.

Biodiversity Metrics

- **Richness:** # of different species
- **Simpson's Dominance (diversity):**

$$D = \sum_{s=1}^{S} p_s^2$$

- **Evar (evenness):**

$$E_{var} = 1 - 2/\pi \arctan \left\{ \sum_{s=1}^{S} \left(\ln(x_s) - \sum_{t=1}^{S} \ln(x_t)/S \right)^2 \Big/ S \right\}$$

- **Berger-Parker Dominance:** proportional abundance of the most dominant species